

## ALTERED PHOTOCYCLIC REGIMES INFLUENCE THE DURATION OF MATERNAL CARE IN A BURROWER BUG (HETEROPTERA: CYDNIIDAE)<sup>1</sup>

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**ABSTRACT.** Female burrower bugs, *Sehirus cinctus* (Heteroptera: Cydnidae), terminate egg care after a predictable interval when eggs do not hatch. This study examined the influence of light/dark (L:D) cycling on the termination of care. Females kept under rapidly cycling light/dark periods (15L:3D) did not differ from controls (15L:9D), with both groups terminating care 8 days after anticipated hatch. In contrast, females kept under slowly cycling light/dark periods (15L:15D) remained responsive for 2 additional days. In terms of the number of light/dark cycles experienced, however, females under slowly cycling light/dark periods (15L:15D) were similar to controls (15L:9D), with both groups terminating care 8 photoperiods after anticipated hatch. In contrast, females kept under rapidly cycling light/dark periods (15L:3D) remained responsive for 2 additional photoperiods. The results of this study suggest that insect subsocial behavior is influenced by metabolic and photoperiodic cues.

*Sehirus cinctus* Palisot (Heteroptera: Cydnidae) is a subsocial burrower bug that exhibits well-defined maternal behavior. Females guard eggs and first-instar nymphs in small burrows, responding defensively to intruders by shielding the offspring with their bodies (Sites & McPherson 1982; Kight 1996). Immediately after eggs hatch, females forage and provision the burrow with host plant fruits (*Prunella vulgaris*: Labeaceae). Several days later, nymphs disperse and maternal behavior ends.

The primary cues governing the termination of care are associated with egg hatching (Kight 1997). However, when mature eggs are experimentally replaced with immature stimulus eggs, females continue brooding past the normal period of care, but consistently terminate care after a predictable period of time (Kight 1997). Under such conditions, the cues normally associated with egg hatching are absent, and termination of parental care appears to be governed by a time-sensitive endogenous process.

The duration of maternal behavior could be influenced by an internal clock, external cues, or a combination of both (reviewed by Saunders 1982). Because the cycling of day and night provide a readily available cue, the predictable duration of care among egg-replaced female *S. cinctus* could be a function of cumulative photoperiod (Goryshin & Tyshchenko 1974; Gibbs 1975; Veerman & Vaz Nunes 1984). Studies of cumulative photoperiod effects have most often examined induction or termination of diapause (Williams & Adkisson 1964; Goryshin & Tyshchenko 1973; Veerman & Vaz Nunes

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1987; Hardie 1990; Numata 1992; Vaz Nunes & Hardie 1993, 1994), although a similar mechanism could potentially govern the termination of care in some insects.

In this study I examine the hypothesis that light/dark cycling influences the duration of care in egg-replaced *Sehirus cinctus* females.

## MATERIALS AND METHODS

Adult *Sehirus cinctus* were collected in Monroe County, Indiana, USA and housed in mixed-sex groups at 25°C and a 15L:9D light/dark photocytle in ventilated petri dishes containing moist sand and fed fruits of the host plant *Prunella vulgaris*. After oviposition, experimental subjects were transferred to individual enclosures and placed in environmental chambers with adjustable photoperiod.

**Control.** Immediately after oviposition, control females were isolated at 25°C in 15L:9D chambers. Shortly before hatching, mature eggs were replaced with immature eggs recently laid by donor females. Females do not discriminate between their own eggs and strange eggs placed in the nest (Kight 1995); hence, this cross-fostering technique was useful for examining the duration of maternal behavior when mothers do not experience egg hatching. Subjects were observed for 10 days after their own (removed) eggs hatched (PH = post-hatch).

**Altered Photocycles.** To examine the influence of light/dark cycling on maternal care, a group of egg-brooding females was held at 25°C, with a 15L:3D photoperiod (fast-cycle 18h females). A similar group was held at 25°C and 15L:15D (slow-cycle 30h females). Shortly before hatching, mature eggs in both treatment groups were replaced with immature eggs recently laid by donor females. In the 10 days after their own (removed) eggs hatched, subjects kept on 18h cycles experienced 13 light/dark cycles, whereas those under 30h cycles experienced 8 light/dark cycles.

I measured maternal responsiveness in all treatment groups with a daily behavioral assay of each female's response to disturbance (Kight 1996). Daily trials were conducted over a range of four hours to ensure that all insects were under scotophase during observations. Subjects were gently touched five times with a dissecting probe on the posterolateral margin of the abdomen at 30 s intervals. Females responded in one of three ways: defense (moving toward the probe), retreat (moving away from the probe), or stasis (no response). By assigning a numeric value to each response (+1 defense, 0 stasis, -1 retreat), a daily score was calculated ranging from -5 (always retreating) to +5 (always defending). All subjects were tested in this manner for 10 days PH.

Each treatment group contained 20 females. Data were analyzed using nonparametric statistical procedures (Siegel & Castellan 1988) with  $\alpha = 0.05$ .

## RESULTS

Maternal response scores (Fig. 1) of control (15L:9D) females never differed significantly from those of fast-cycle (15L:3D) females (Wilcoxon-Mann-Whitney Test,  $N=20$ ,  $P>0.0856$  for all days), but were significantly lower than those of slow-cycle (15L:15D) females on day eight PH (Wilcoxon-Mann-Whitney Test,  $N=20$ ,  $P=0.0212$ ) and marginally lower on day nine PH ( $P=0.0661$ ).

There was, however, a pronounced difference between the photocyclic extremes (Fig. 1). Maternal response scores of fast-cycle (18h) females began to fall on day eight PH, and were significantly lower than those of slow-cycle (30h) females after and including day nine PH (Wilcoxon-Mann-Whitney Test,  $P \leq 0.0197$  for days nine to ten PH).

Duration of maternal responsiveness was therefore influenced by the rate of light/dark cycling in that females experiencing abnormally long (30h) cycles remained responsive for 24 to 48h longer than either control females or females under short (18h) cycles.

When data were examined in terms of the number of *experienced* light/dark cycles, both slow-cycle (30h) females and control females experienced approximately 7 cycles PH before terminating care (Fig. 2). Fast-cycle (18h) females, however, remained responsive for 9 cycles PH—two more than controls and slow-cycle (30h) females. Thus fast-cycle (18h) females remained maternal for more cycles than expected from control data.

## DISCUSSION

The life history of *Sehirus cinctus* may demand reliable mechanisms to determine duration of care. Reproduction is synchronized with availability of the host plant, which flowers for only several weeks each spring (Kight 1995). Pre-reproductive females feed on developing host plant fruits, and by the time oviposition occurs fruits have matured and fallen from the plants. When eggs hatch, fruits remain available, but *Prunella vulgaris* is rapidly displaced by other spring annuals and the source of provisions diminishes (Kight 1996). Should eggs fail to hatch, females could suffer reduced fitness if a replacement clutch is not initiated before the food source disappears.

There is evidence in other species that internal mechanisms govern the duration of care given to offspring. For example, female burying beetles, *Necrophorus vespilloides*, respond maternally to conspecific stimulus larvae only during the anticipated hatching period of their own young (Müller & Eggert 1990). Stimulus larvae presented to the mother either too early or too late are killed by her, but larvae introduced at the time of hatching elicit maternal care from her. Similar behavior is found in male house mice, *Mus domesticus*, which generally attack and kill stimulus pups, but show inhibi-

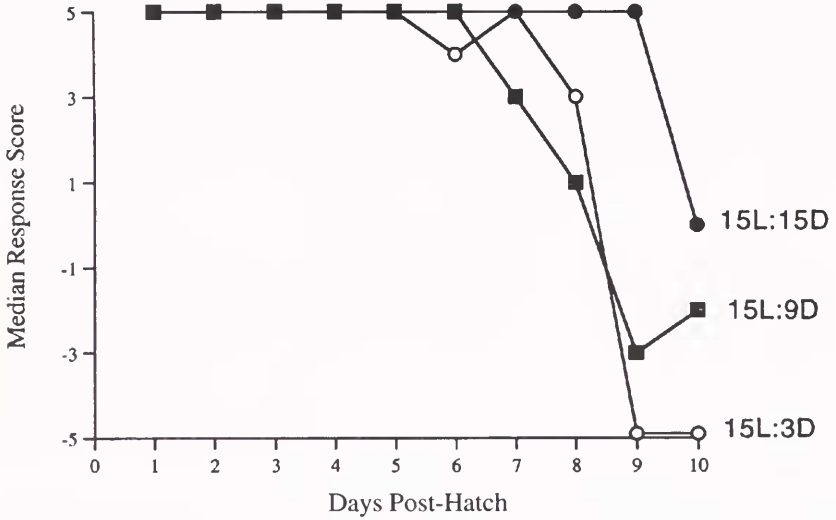


Figure 1. Median maternal response scores of cross-fostered brooding mothers kept under different photocyclic regimes.

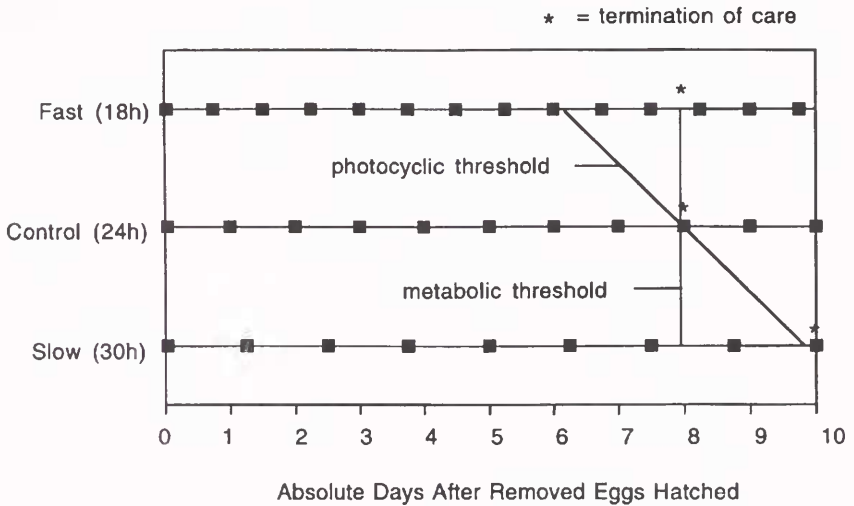


Figure 2. Time-line of experienced photoperiods for brooding females kept under cycles of different length. Distance between squares is one cycle. Photocyclic threshold (diagonal line) refers to the predicted minimum number of light/dark cycles prior to termination of care. Metabolic threshold (vertical line) refers to the predicted minimum number of absolute days prior to the termination of care. Asterisks indicate when termination actually occurred.

tion of infanticidal behavior at a predictable time after mating. Moreover, the interval between ejaculation and inhibition of infanticide in mice coincides with the gestation period of potentially sired young (Perrigo et al. 1990). This interval can be shortened or lengthened by placing mice under non-24 h light/dark cycles (Perrigo et al. 1990, 1992).

The results of the present study indicate that the duration of egg care in *Sehirus cinctus* is similarly influenced by light/dark cycles. In terms of absolute time, females experiencing 18h or 24h cycles terminated care 24-48 h earlier than females experiencing 30h cycles. However, if females based the termination of care exclusively on the number of light/dark cycles experienced, 18h cycle females should terminate care earlier than controls, but this did not occur.

One possible explanation is that the mechanism is metabolically compensated—females may terminate care when sufficiently hungry. At 25°C, threshold metabolic demand (hunger) would have occurred in control females 7 absolute days after their own (removed) eggs hatched. Fast-cycle (18h) females continued brooding for 9 cycles and 7 days PH, which is consistent with the metabolic demand hypothesis: females became sufficiently hungry at 7 days PH, regardless of the number of cycles perceived. This hypothesis is supported by evidence that maternal females terminate care earlier when housed at warmer ambient temperatures (Kight & Cseke 1998) and anecdotal observations of egg-replaced females leaving the burrow to gather single fruits for their own consumption, always within 24 h of termination of care. Metabolic demand and maternal motivation may be competing processes.

Slow-cycle (30h) females, however, remained responsive for 7 cycles but 9 days PH, indicating that metabolic demand is not sufficient for the termination of care. Because all treatment groups were housed at the same ambient temperature, slow-cycle (30h) females had metabolic demands similar to fast-cycle (18h) and control females at 7 days PH. That slow-cycle females remained maternal for additional absolute time indicates that a minimum number of photocycles must also be experienced prior to termination of care, although it is possible that metabolic demand would eventually circumvent this minimum under more extreme photocyclic conditions (i.e. longer cycles or constant light/dark).

An alternative explanation for these findings is that slow-cycle females would reach a metabolic threshold less quickly if metabolic expenditure decreases at night. If, for example, maternal females were more vigilant during the day, slow-cycle females, which did not experience as many photocycles as the other groups by day 7 PH, would have expended less cumulative energy. Brooding females in all treatment groups, however, were generally slow to



respond to the initial experimental stimulus of each daily trial but responded immediately to subsequent stimuli, suggesting that daytime metabolic expenditure is minimal prior to disturbance.

The results of this study indicate that egg-replaced burrower bugs kept at 25°C do not terminate care until both 7 absolute days and 7 photocycles PH have passed. While these events occur simultaneously under natural circumstances, both conditions were met before termination of care even when absolute time and photocycle were experimentally uncoupled (Fig. 2).

Because post-hatching maternal provisioning of food is important for offspring survival, reproductively successful females should not terminate care early. *S. cinctus* thus appears to have evolved a mechanism to prevent maladaptively premature termination of care. The present study represents the first demonstration that insect parental behavior is influenced by cumulative light/dark cycling.

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## BOOKS RECEIVED AND BRIEFLY NOTED

THE BIOMECHANICS OF INSECT FLIGHT. FORM, FUNCTION, EVOLUTION. 2000. Robert Dudley. Princeton University Press. 476 pp. Hard. \$49.50.

Beginning from an overview of insect flight biomechanics, this author goes on to explain insect morphology, wing motions, aerodynamics, flight energetics, and flight metabolism within a modern phylogenetic setting. Drawing on biomechanical principles, he describes and evaluates flight behavior and the limits to flight performance, and develops evolutionary explanations of insect flight. He analyzes the origins of flight in insects, the roles of natural and sexual selection in determining how insects fly, and the relationship between flight and insect size, pollination, predation, dispersal, and migration. The main focus of the text is the author's explanation of functional design from evolutionary and ecological perspectives. Also noteworthy is the synthesis of literature (over 100 pp.) on insect flight.

THE TIGER BEETLE GENUS OXYCHEILA (INSECTA: COLEOPTERA: CICINDELIDAE). 1999. J. Wiesner. COLEOPTERA. Schwanfelder Coleopterologische Mitteilungen. Schwanfeld, Germany. 81 pp. 4 color plates. 8 $\frac{1}{2}$  x 11. Paper.

A complete systematic revision of the genus. 46 species are included. For each species, the following are presented: synonymies, type specimen or status, diagnosis, description or re-description, distribution, localities, ecology, and etymology. 55 diagnostic figures. 48 specimens illustrated on 4 color plates.